A NEW DEEP-WATER HYDROTHERMAL SPECIES OF *NUCULANA* (BIVALVIA: PROTOBRANCHIA) FROM THE GUAYMAS BASIN

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ABSTRACT

A new deep-water species of *Nuculana* is described that occurs in the southern trough of the Guaymas Basin and is associated with a hydrothermal vent system. The species, *N. grasslei,* is characterized by a large, ornamented prodissoconch, but in other respects it differs little in its gross morphology from other species of *Nuculana*. Such specializations that do occur relate to the hostile sulphurous environment in which it lives. Particularly important in this regard is the thickened periostracum and the large volume of pigmented blood.

Keywords: *Nuculana*, Protobranchia, hydrothermal vents.

INTRODUCTION

This paper describes the gross morphology of a new species of *Nuculana* taken from the southern trough of the Guaymas Basin in the Gulf of California at a depth of 2000 m, adjacent to a position where hydrothermal fluid at between 270–314°C percolates through a thick layer of pelagic sediment and through chimneys (Lonsdale et al., 1980; Simoneit & Lonsdale, 1982; Grassle et al., 1985; Berg & Van Dover, 1987).

Juvenile and adult specimens were taken during a series of dives by DSRV Alvin in January 1982 and August 1985 (listed in Jones, 1985, and Berg & Van Dover, 1987). In the Guaymas Basin, there are black smokers, and the sediments from the study area smell strongly of hydrogen sulphide. On this sediment, large patches of the filamentous bacterium *Beggiatoa* are present. The soft sediment benthic communities comprise a few species in great numbers, but their composition varies over short distances (Grassle et al., 1985). Samples of plankton containing larvae of the *Nuculana* were taken within the 5 m of water column above the sea bed (Berg & Van Dover, 1987). The methods employed to collect the specimens are reported by Grassle et al. (1985) and Berg & Van Dover (1987).

I am very grateful to Dr. J. Frederick Grassle for allowing me to examine this material, to Dr. Cindy Lee Van Dover for permission to copy from SEM photographs of larvae, and to the director and staff of the Woods Hole Oceanographic Institution for their help over many years.

DESCRIPTION

Genus *Nuculana* Link 1807
Type species (OD):
    Arca rostrata Brugière, 1789,
    ex Chemnitz MS, = *Arca pernula*
        Müller, 1779.

Shell robust, moderately and posteriorly elongate; rostrum truncate, usually bicarinate, moderately compressed, strong concentric sculpture; umbo anterior; posterior ventral margin slightly sinuate, occasionally with radial ribs; escutcheon present; hinge teeth chevron-shaped; ligament external with central internal part.

Nuculana grasslei, new species

Type locality: Guaymas Basin, south trough, 27°03′N, 111°23′W, 2003 m.

Holotype: USNM   1 specimen
    No. 859482

Paratypes: USNM   specimens selected
    No. 859481   by J. A. A. from the type
            locality.

Named in honour of Dr. J. F. Grassle, friend and colleague of many deep-sea voyages and participant in the Guaymas Expedition.

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Material

Dive No.	Depth (m)	Specimens Examined	(Number Collected)	Position	Equipment	Date
Alvin 1168	2003	25	(50)	27°03'N, 111°23'W	SS	10–1–82
		3	(3)		TC	
Alvin 1169	1998	8	(16)	27°03'N, 111°25'W	BC	11–1–82
Alvin 1170	2019	—	(7)	27°01'N, 111°25'W	BC	12–1–82
Alvin 1174	2011	—	(1)	27°01'N, 111°24'W	BC	17–1–82
Alvin 1175	1997	—	(1)	27°03'N, 111°23'W	BC	18–1–82
Alvin 1176	2022	4	(152)	27°01'N, 111°25'W	TC	19–1–82
Alvin 1607	2012	4	(4)	27°05'N, 111°24.5'W	TC	29–7–85
Alvin 1608	2002	1	(1)	27°07'N, 111°24.4'W	TC	31–7–85
Alvin 1614	2004	2	(2)	27°07'N, 111°24.4'W	BC	6–8–85
Alvin 1628	2000	—	(5 postlarva)	27°00'N, 111°24.5'W	PT	23–8–85
(1–5 above bottom)						
Alvin 1629	2000	—	(1 postlarva)	27°00'N, 111°25.5'W	PT	23–8–85
(3–4 above bottom)						

BC—Box Core (225 cm² area sampled)
TC—Tube Core (35 cm² area sampled)
SS—Scoop Sample (63 mm mesh bag over metal frame) non-quantitative
PT—Plankton Tow (0.4 m², 183 μ mesh) non-quantitative

Samples reported in Grassle et al. (1985) and Berg & Van Dover (1987).

Shell Description (Figs. 1–4)

Shell elongate, stout, bluntly rostrate, equivalve—although central portion of ventral margin of right valve may slightly overlap left valve as a consequence of strong concentric ornamentation; broad concentric ridges extend over central region of shell from faint posterior radial ridge to close to anterior margin, those close to umbonal region less conspicuous than those ventral to them; fine, closely spaced concentric striae extend anterior and posterior to ridges, with line of ridges marked by heavier striae; two faint radial ridges extend from umbo to posterior ventral margin; umbo anterior (position at approximately 38% total length), relatively large, beaks inturned; antero-dorsal margin smoothly curved near umbo, but in large specimens somewhat flattened anteriorly; postero-dorsal margin more or less straight or even slightly concave in large specimens, angulate at point opposite posterior limit of hinge plate; posterior margin broadly truncate and slightly gaping; ventral margin for most part an even, shallow curve, except posteriorly between limits of radial ridges, where it is sinuate (this corresponds to position of feeding aperture); escutcheon and lunule outlined by faint ridges; hinge plate moderately broad, continuous ventral to umbo; hinge teeth chevron-shaped, number increasing with increasing shell length, 17 anterior and 25 posterior teeth in specimen 26.3 mm total length, of these 6 or 7 on each side of umbo are more leaf-like than those more posterior, 11 anterior and 15 posterior in specimen 13.7 mm total length; ligament predominantly opisthodetic, small internal part attached to resilium, which occupies a dorsal position on hinge plate and separates anterior and posterior hinge tooth series; external part comprises small portion anterior to umbo and moderately elongate portion posterior to umbo, latter somewhat extended by fused periostracum; periostracum golden-yellow, much thickened and strongly held within periostracal groove.

Prodissoconch large, 275–283 μm total length, ornamented with 9–10 reticulated concentric ridges and 10–11 radial reticulations.

Length of largest shell examined: 26.3 mm.

Internal Morphology

The gross morphology of the body organs is typically nuculanid in form (Fig. 5) and differs little from descriptions of shallow-water species (Yonge, 1939).
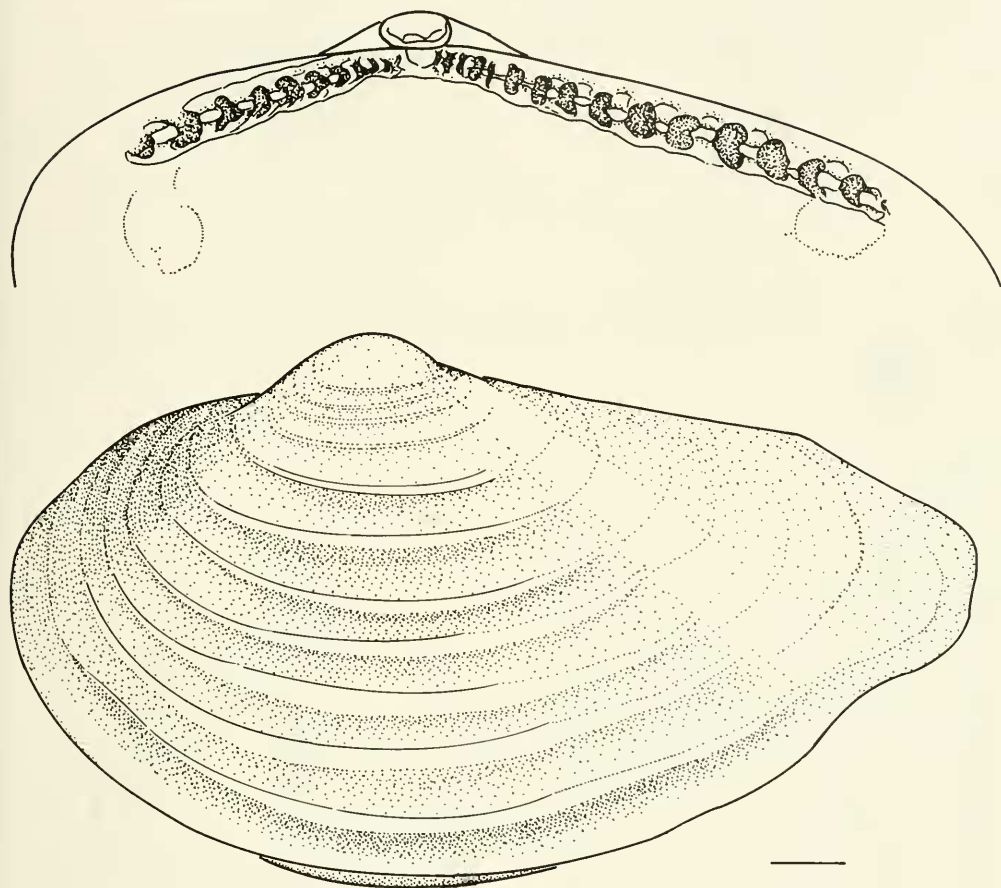
FIG. 1. *Nuculana grasslei*. Lateral view of the shell of the holotype from the left side and an internal view of the hinge region of the right valve of a specimen of similar size (bar = 1 mm).

The mantle is relatively unspecialized. Three typical folds are present at the mantle margin. Antero-ventrally the middle sensory fold is somewhat enlarged to form a simple anterior sense organ. Posteriorly there is a shallow siphonal embayment enclosing combined inhalent and exhalent siphons. The inhalent siphon is unfused both dorsally and ventrally (Fig. 6). Nevertheless, the integrity of the siphonal lumena is maintained by the apposition of thickened central and ventral longitudinal ridges on the inner siphonal surface. The inhalent siphon is somewhat shorter than the exhalent. There is no siphonal tentacle present, as is the case in other species of *Nuculana* (e.g. Yonge, 1939); however, a small lobe is present at the posterior limit of the left and right inner mantle folds where they meet the ventral margins of the

mantle embayment. These are not homologous to the protobranch tentacle and probably represent the termination of the main rejection tract of the mantle that is present on the inner surface of the inner muscular mantle fold. Their function presumably is to guide pseudofaeces to the inhalent siphon so they may be ejected on contraction of the shell valves. There is a simple feeding aperture immediately anterior to the siphonal embayment. Here the middle sensory and the inner muscular lobes of the mantle are widened and somewhat folded. The feeding aperture of *N. grasslei* is much simpler than that of many deep-sea nuculanid protobranchs (Allen & Hannah, 1989). Numerous fine radial muscles are present within the mantle to the inside of the marginal folds. The adductor muscles are relatively small and unequal in
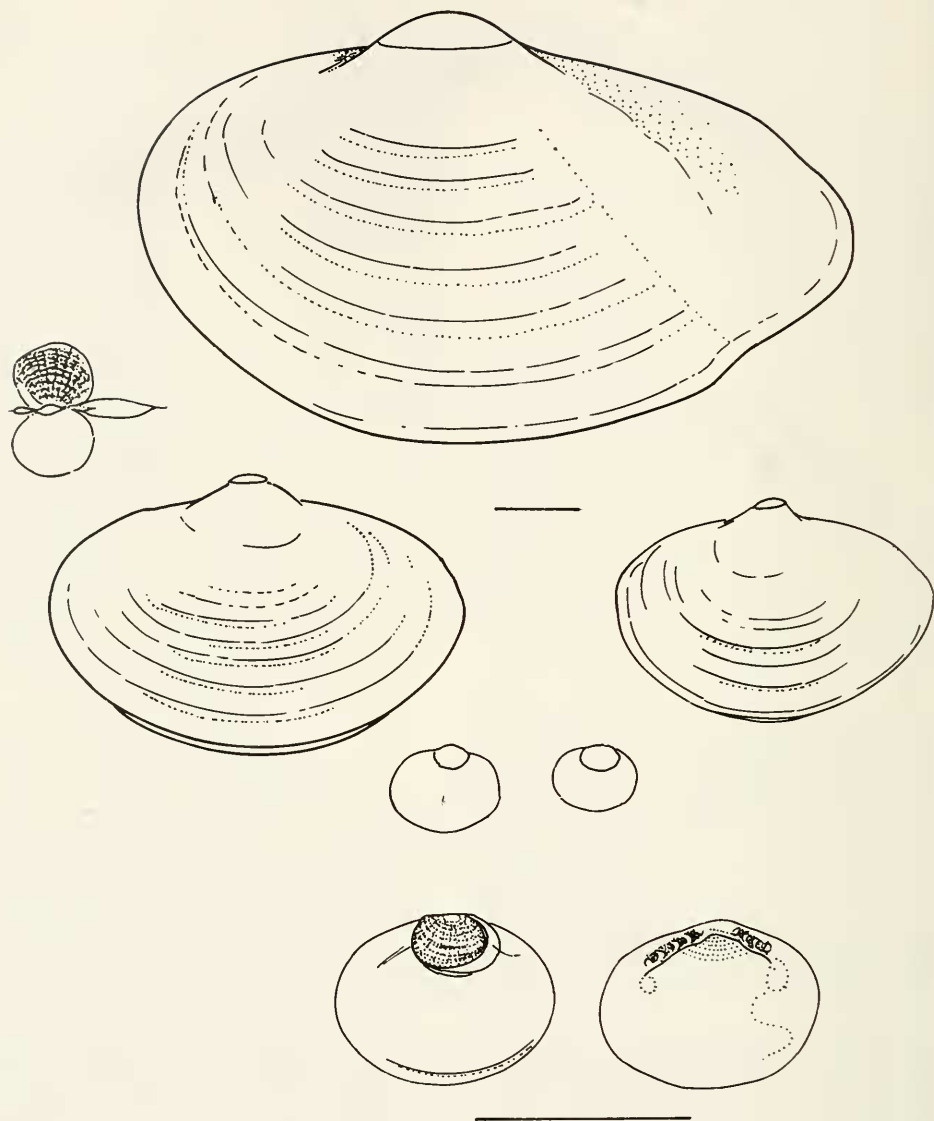
FIG. 2. *Nuculana grasslei*. Lateral views of shells from the right side to show variation in shape with increasing shell size. The figure includes a dorsal view of the hinge region of the next but largest shell illustrated and enlarged internal and external views of valves of a juvenile shell (bars = 1 mm).

size. The posterior muscle is oval in cross section, with "quick" and "catch" portions of equal size. The anterior muscle is crescent-shaped, with a narrow elongate "catch" portion running the length of the anterior face.

The gills are well developed and extend horizontally and parallel to the postero-dorsal shell margin from the mid-visceral region to the siphonal embayment. In the largest spec-

imen examined, there are approximately 150 broad gill plates on each demibranch. These are comparable to those described by Yonge (1939). The plates of each demibranch alternate in their attachment to the axis. Each axis extends posteriorly beyond the posterior plate as an extremely long, fine filament. Unlike the condition in other nuculanid protobranchs, these do not appear to be attached to the
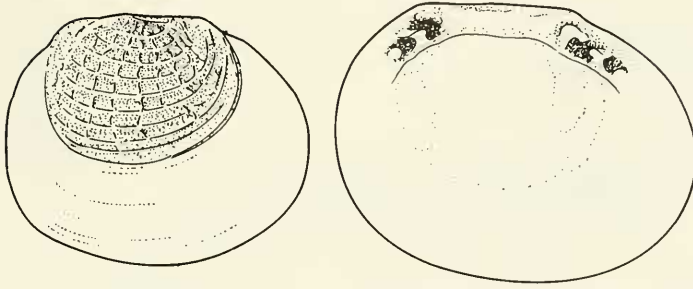
FIG. 3. *Nuculana grasslei*. Drawing from SEM photographs of the lateral external surface of the left valve and the internal surface of the right valve of a planktonic postlarva (with kind permission of Dr. C. L. Van Dover) (bar = 0.1 mm).
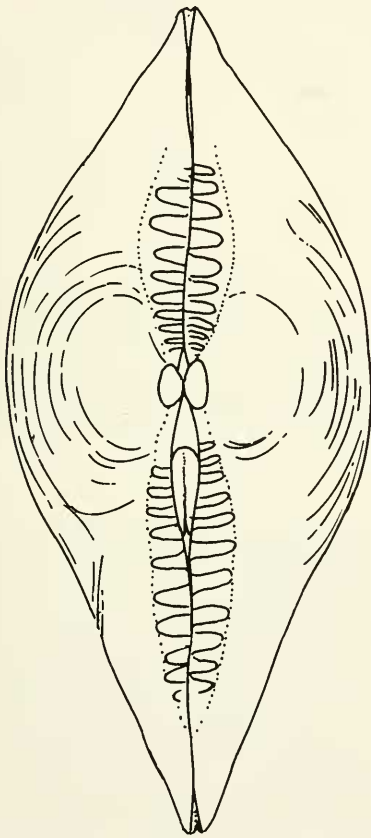

FIG. 4. *Nuculana grasslei*. Dorsal view of shell to show external detail of hinge region (bar = 1.0 mm).

respective left and right central ridges separating the inhalent from the exhalent siphon. Whether this is a consequence of preservation and a tenuous attachment has been lost cannot be determined at present. They presumably act as do axial extensions in other protobranchs, as guides to the transport of faecal rods from anus to exhalent siphon. It may be speculated that in this particular case they have become greatly extended to ensure disposal far distant from the feeding aperture.

The palps are moderate in size, with relatively broad sorting ridges on their inner faces. As in the case of the gill plates, the number of ridges on each face varies with the size of the specimen—39 in a specimen 26.3 mm total length and 14 in a specimen 3.0 mm total length. The palp proboscides are broad and long, even in the contracted, preserved state. In life they must be capable of considerable extension beyond the shell.

The foot and viscera are extensive. The muscular foot is broad. The sole is deeply divided and fringed with papillae. There is a small "byssal" gland in the heel of the foot at the point where it joins the sole. The pedal retractor muscles are not particularly well developed. There is a posterior pair inserted antero-dorsal to the posterior adductor muscle and two pairs of anterior retractor inserted postero-dorsal to the anterior adductor muscle.

The mouth lies somewhat posterior to the ventral edge of the anterior adductor muscle. The oesophagus is elongate and opens dorsally on the anterior face of the stomach. The stomach and combined style sac are moderately large and lie vertically within the body. Because of the brittle nature of the preserved specimens and because the digestive diverticula adhere closely to the stomach wall, little detail of the stomach was observed. Nevertheless, a well-developed dorsal hood and an extensive gastric shield are present. A small number of grooves comprising the posterior sorting area were identified. There is no doubt
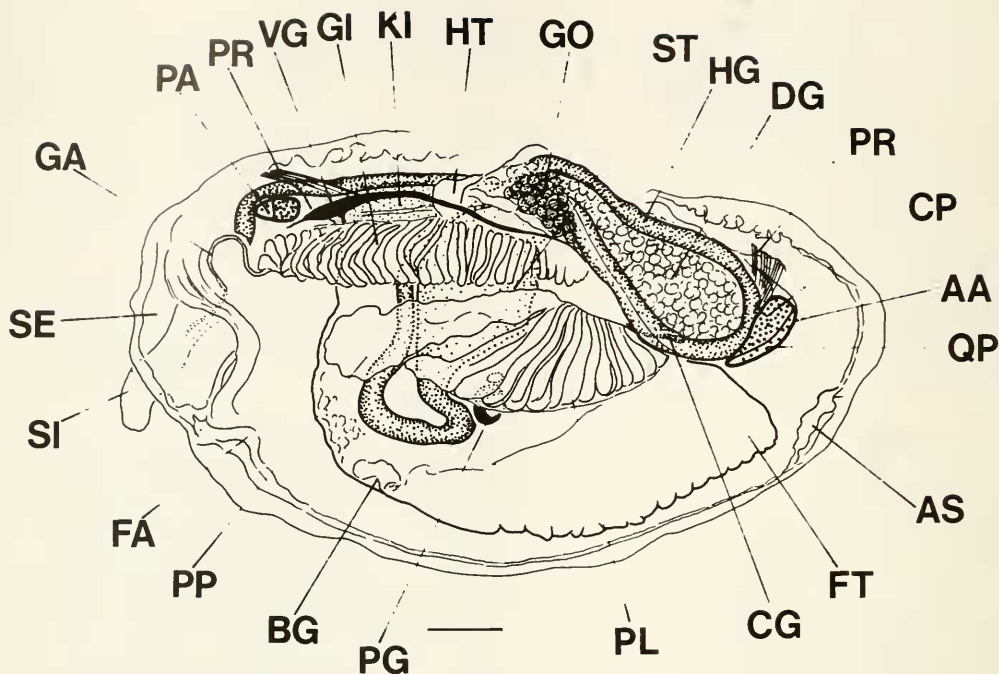
FIG. 5. *Nuculana grasslei*. Semidiagrammatic drawing of the internal morphology of a specimen from the right side (bar = 1.0 mm). AA, anterior adductor muscles; AS, anterior sense organ; BG, "byssal" gland; CG, cerebral ganglion; CP, "catch" portion of adductor muscle; DG, digestive diverticula; FA, feeding aperture; FT, foot; GA, extension of gill axis; GI, gill; GO, gonad; HG, hindgut; HT, heart; KI, kidney; PA, posterior adductor muscle; PG, pedal ganglion; PL, palp; PP, palp proboscis; PR, pedal retractor muscle; QP, "quick" portion of adductor muscle; SE, siphonal embayment; SI, combined siphon; ST, stomach; VG, visceral ganglion.
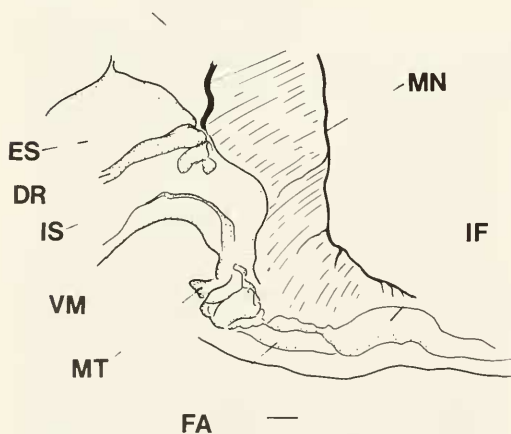

FIG. 6. *Nuculana grasslei*. Enlarged detail of the siphon and postlarval margin of the left mantle (bar = 0.1 mm). DR, dividing ridge; ES, exhalent siphon; FA, feeding aperture; IF, inner mantle fold; IS, inhalent siphon; MT, mantle tentacle; SN, siphonal nerve; VM, ventral margin of inhalent siphon.

that the morphology of the stomach differs little from the typical deep-sea nuculanid stomach (Allen & Hannah, 1989). The hindgut takes a typical course. From the style sac, it passes posterior to the stomach to the dorsal margin of the viscera. It then describes a loop on the right side of the body (Fig. 7), reaching the internal face of the anterior adductor muscle before passing posteriorly along the mid dorsal margin of the body, through the pericardium and ventricle of the heart, over the posterior adductor muscle to the anus. There is a typhlosole along the length of the hindgut; the faecal rods are typically compact with a groove moulded by the typhlosole. The digestive diverticula are very extensive with fine tubules that permeate the entire visceral mass.

The heart is exceptionally large. Paired lateral auricles are each supplied anteriorly via a major vessel from the gill axis. The blood volume also appears to be large. In all specimens, the contraction of the body on preser-
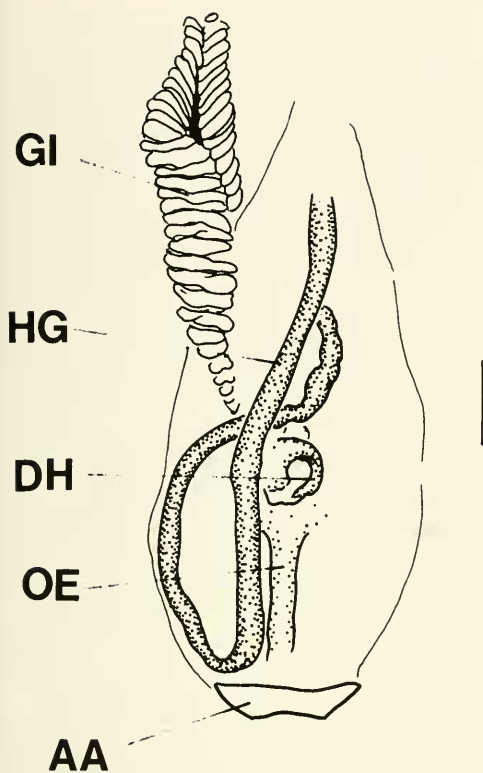
FIG. 7. *Nuculana grasslei.* Dorsal view of the internal morphology of a specimen to show the course taken by the hind gut and the disposition of the right gill (bar = 1.0 mm). AA, anterior adductor muscle; DH, dorsal hood; GI, gill; HG, hind gut.

vation has forced blood to various parts of the body, particularly the sinuses of the mantle margin and the gill and gill axis. These are swollen with congealed red-pigmented blood.

The kidney consists of paired brown-pigmented intercommunicating sacs, lying between the heart and the posterior adductor muscle. It is particularly well developed.

The nervous system follows the typical protobranch plan. The paired cerebral ganglia are slender and not well developed. Similarly, the visceral ganglia, although somewhat larger than the cerebral, are also small in comparison with other deep-sea nuculanids. From each visceral ganglion, there is a major nerve to the gill axis, to the siphon, and to the mantle edge (Fig. 5). The pedal ganglia are large and lie at the interface of foot and viscera, anterior and close to the ventral limit of the hindgut.

Paired gonads were seen in specimens >18 mm total length. The major portion of the gonad lies anterior to the heart and dorsal and posterior to the stomach. From there, it spreads thinly across the lateral surface of the digestive gland. The gonadial ducts traverse the lateral faces of the kidney to open in the supramantle cavity. No fully mature gonad was present in the specimens examined.

Shell Growth

Because of the wide difference in the size of the specimens examined, it was possible to obtain some information on the change in shape of the shell with increasing size.

The prodissoconch is oval and large (275–283 μm total length) equivalve and approximately equilateral (Fig. 3). The prodissoconch of the post-larva illustrated by Berg & Van Dover (1987), and by kind permission redrawn here for comparison with the prodissoconchs present on the adult shells, has a reticulated ornamentation that is presently without parallel in the Protobranchia and almost so in bivalves in general.

Post-prodissoconch shell growth immediately begins to take on adult proportions. The anterior growth is less than the posterior, and the disparity in the numbers of teeth on the hinge plates is immediately apparent, with two anterior and three posterior teeth present in the smallest post-larval shells (480 μm total length) in the collection. The teeth are on a broad and continuous hinge plate (Figs. 1, 2). The outline of the shell gradually changes with growth, and by the time the shell is 10 mm long the adult proportions are established (Figs. 2, 8). Thus, the percentage ratio of height over length to length over the first five millimeters of growth changes from 75% to 65%. At the same time, the shell becomes more rostrate, with the post-umbonal length increasing in relation to total length, while the shell becomes more slender. This change in shape with size is typical of all deep-sea protobranchs (Allen & Hannah, 1989).

With increasing size (age), the umbonal region of the shell becomes increasingly eroded. All specimens of more than 10 mm total length show erosion to some degree. In the case of the larger specimens (Fig. 9), an area equivalent to the outline of a 10-mm shell may be affected and to such an extent that all that remains is the thin innermost layer of shell. In this extreme condition, the umbo is completely lost, with the ligament and the remains of the hinge plate in which the hinge
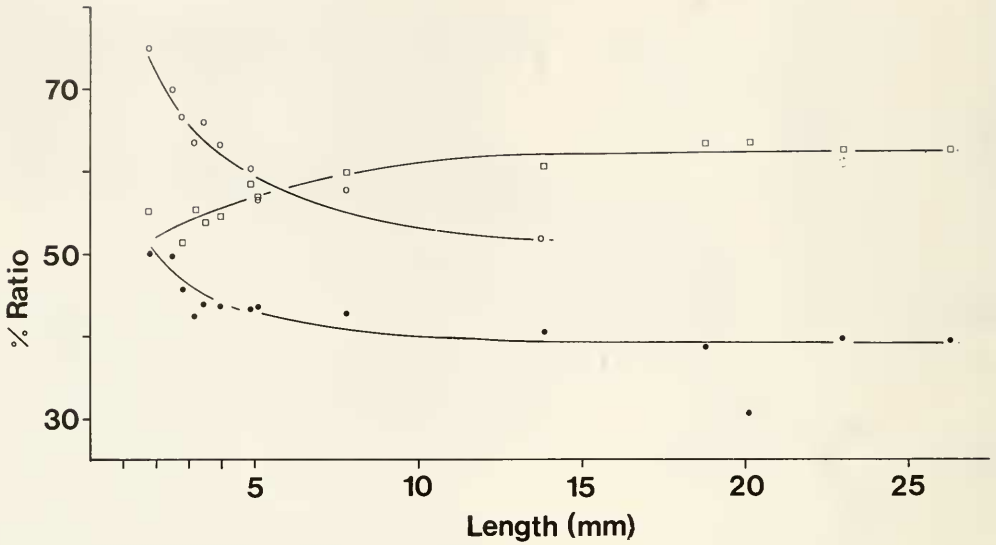
FIG. 8. *Nuculana gasslei*. Plot of the percentage ratios of height to length (open circles), width to length (closed circles) and post umbonal length to length (open squares) against length.
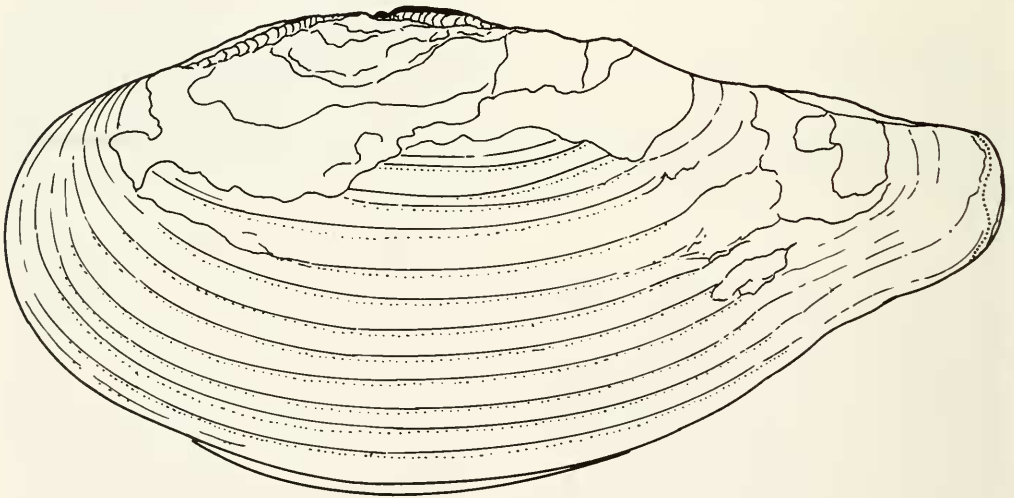

FIG. 9. *Nuculana grasslei*. Lateral view of a large shell from the left side to show the extent of corrosion (bar = 1.0 mm).

teeth are clearly visible, standing out as a crest to the shell (Fig. 9). In addition, the area over the insertion of the posterior adductor muscle also becomes eroded.

Comparisons have been made with known species, with particular attention being paid to those from off the Pacific coast of America and from deep water. The combined shell characters of *N. grasslei* are unlike those of any other described species (Abbott, 1974; Bernard, 1983; Dall, 1890, 1896, 1897, 1908, 1916; Dall & Bartsch, 1910; Hertlein & Strong,

1940; Moore, 1983; Oldroyd, 1935; Willett, 1944). The main points of recognition of *N. grasslei* include the shell outline, in which the postero-dorsal margin is angulate and the postero-ventral margin is sinuous, the large and anteriorly placed umbo, the slightly flattened antero-dorsal margin, and the form and spacing of the concentric ribs. Furthermore, no other description includes reference to an ornamented prodissoconch, though this does not preclude unnoted occurrence in other species. It must be said that the prodissoconch in *N. grasslei* is striking, and a similar presence in other species is unlikely to have been overlooked by earlier authorities.

Although large by deep-sea protobranch standards (few species obtain a length of more than 5 mm), *N. grasslei* is not large in comparison with other species of *Nuculana*. For example, *N. pernula* (Müller, 1779) from shallow Arctic seas is similar in size, as too is *N. taphria* Dall, 1897, from the shallow water of California and Baja California.

Discussion

The investigation reported here is limited to the gross morphological description of a new deep-sea hydrothermal species. Detailed microscopical examination was not made in the knowledge that Dr. Richard Gustafson of Rutgers University was studying various organs in detail.

For the most part, the functional morphology of *N. grasslei* differs little from that of other species of *Nuculana* from slope or shelf seas. There are no characters that differ so significantly to warrant separation at generic level. Nevertheless, there are a few unusual characters that relate to the habitat of the species and at least one that is unrelated to the habitat of the adult. The former include the thick periostracum and the large volume of pigmented blood; the latter refers to the ornamented prodissoconch.

The periostracum varies in thickness but measures up to 40 μm a figure that is twice that of *N. minuta* (Müller, 1776) of a similar size (pers. obs.). It is probable that the thickened nature of the periostracum relates to the sulphurous nature of the habitat. Muds smelling of hydrogen sulphide must be acidic and thus corrosive to the shell. The thickened periostracum clearly protects the shell up to a third of the life of the animal as measured by shell length, i.e. to the size when gonads are developing. Similarly, the large blood volume

must also relate the the nature of the habitat. Hydrogen sulphide will affect oxygen levels of the overlying sea water as well as that within the sediment. A large oxygen carrying capacity of the blood would be expected on *a priori* grounds. It is known that protobranchs in particular can survive anoxic conditions for long periods of time (Doeller et al., 1988; pers. obs.). Thus, all things being equal, it would be expected that protobranchs could survive the conditions pertaining at seeps and vents with little modification. In fact, there is circumstantial evidence that protobranchs can survive reducing conditions in marine muds better than most bivalves, possibly with the exception of members of the Lucinacea. In recent laboratory experiments, three species of *Nucula* have survived anoxic conditions for more than three weeks (pers. obs.).

Although common to all species of *Nuculana,* the lack of the siphonal tentacle is perhaps of interest, as too is the relatively poorly developed nervous system. Again, it may be speculated that this may be preadaptive in that *N. grasslei* lives in sediments in which there is ample food material in the form of bacterial mats at the surface. In such a situation, specialized sensory assistance in food gathering is of minimal importance.

The ornamented prodissoconch is striking. On first reflection, little evolutionary advantage would seem to accrue from this reticulation. As in all bivalves it is protective, not in terms of predation, but in terms of the protection it affords against the dissolution of the shell at a weak and vulnerable point. When the prodissoconch is eventually lost from the surface of the growing adult shell, it exposed a small area of calcium carbonate to the umbo, a part of the shell that is relatively thin. In the case of *N. grasslei,* the prodissoconch remains in place for a relatively long period, protecting the shell against corrosion until the animal is beginning to mature. As soon as it is lost, corrosion occurs at the place where it had been. What function the reticulate ornamentation plays is much less certain. Reticulate ornamentation is characteristic of some protobranchs (e.g. *Nucula sulcata* Bronn, 1831) (Allen, 1954). Whereas in the adult ornamentation may assist in the maintenance of the position of the shell within the sediment (Stanley, 1970), it hardly seems likely in the case of the newly settled prodissoconch.

Unlike better known vent bivalves, *Calyptogena magnifica* Boss & Turner, 1980, and *Bathymodiolus thermophilus* Kenk & Wilson,

1985, *N. grasslei* is not exceptionally large. This may be related to its deposit rather than its suspension feeding habits, its digestive physiology, and to the apparent lack in the gill of symbiotic chemoautotrophic bacteria of the type present in *Calyptogena* and *Bathymodiolus,* although other types of bacteria are present (Gustafson, pers. comm.). These latter may bear relationship to the large volume of pigmented blood observed in the specimens examined. The pigment is almost certainly haemoglobin. This is known to be present in other vent bivalves and in some other nuculanid protobranchs (Wittenberg, 1985). It would appear that this is part of an efficient oxygen carrying system in relatively low oxygen pressures (Wittenberg, 1985).

The large size of the prodissoconch indicates a large heavily yolked egg, probably in the order of 200 + μm. (No adults with mature ova were present in the samples.) It is not unusual for vent invertebrates to have lecithotrophic larvae (Gage & Tyler, 1991). Although this does not appear to restrict the ability of vent species in general to colonize new vents as they occur, at present *Nuculana grasslei* is known only from the Guaymas Basin in the Gulf of California.

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